Z. Säugetierkunde 59 (1994) 366–377

ISSN 0044-3468

Craniometric differentiation and chromosomal speciation of the genus *Proechimys* (Rodentia: Echimyidae)

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Receipt of Ms. 11. 3. 1994
Acceptance of Ms. 16. 6. 1994

Abstract

Multivariate morphometrics have been used to investigate the systematics and geographic variation of the spiny rats of the genus *Proechimys* occurring in Venezuela. These populations exhibit extensive differences in their karyotype from 2n = 24 to 2n = 62, and patterns of differentiation in morphological traits of the skull and of the mandible are consistent with a phylogenetic hypothesis suggesting successive events of speciation coupled with increase in diploid numbers. Although no single character by itself can be used to discriminate between taxa, all species and subspecies are clearly distinguishable from each other in a multivariate context.

Introduction

Spiny rats, *Proechimys* (Rodentia: Echimyidae), is a widely distributed genus occurring in the lowland and premontane Neotropical forests of South America, with many extant named species (Patton 1987; Reig et al. 1980). The entire genus is characterized by a high chromosomal heterogeneity, with diploid numbers ranging from 2n = 14 to 2n = 64 (Reig et al. 1980), and it has been considered as some of the best evidences for genetic change and chromosomal speciation (King 1993).

An exhaustive review of the genus has been provided by Patton (1987), who recognized nine groups of species, primarily based upon morphological traits. According to the classification of Patton (1987) three of these species groups occur in Venezuela, i.e. *trinitatus, canicollis* and *guyannensis*. The range of both *canicollis* and *trinitatus* lies north of the Orinoco river, with only one species of *trinitatus* in the southern part of the basin (*P. hoplomyoides*). The upper Orinoco river groups comprise different species, *P. canicollis* (2n = 24), the only species of the *canicollis* group, and, for the *trinitatus* group, the species *P. trinitatis* (2n = 62), and the nominate superspecies *P. guairae*, with three closely related allospecies: *P. poliopus* (2n = 42), *P. guairae* (2n = 44, 46, 48, 50 and 52) and a third, referred by Aguilera et al. (1994) as *Proechimys* sp. (2n = 62) (Fig. 1).

The superspecies *P. guairae* represents a remarkable example of a typical rassenkreis, occurring in parapatric contiguous ranges skirting the Maracaibo lake and the mountains of Cordillera de la Costa and Cordillera Andina (Fig. 1). The rassenkreis is characterized by karyomorphs with increasing diploid numbers, from *P. poliopus* (2n = 42) to *Proechimys* sp. (2n = 62), providing evidence that led Reig (1980) to hypothesize a model of chromosomal speciation via centric fissions from lower to higher chromosomal numbers.

The species *P. guairae* is polytypic, and comprises different karyotypic races with diploid numbers corresponding to 2n = 44, 46, 50 and 52 (Reig 1989; Aguilera et al. 1994). Not all karyomorphs have been assigned a subspecific name, and some are known from the locality from which chromosome preparations were available. Ranges of chromosomal races are apparently contiguous and parapatric, from the lake of Maracaibo to the Unare basin, along the northern coast of Venezuela (Fig. 1). The chromosomal race

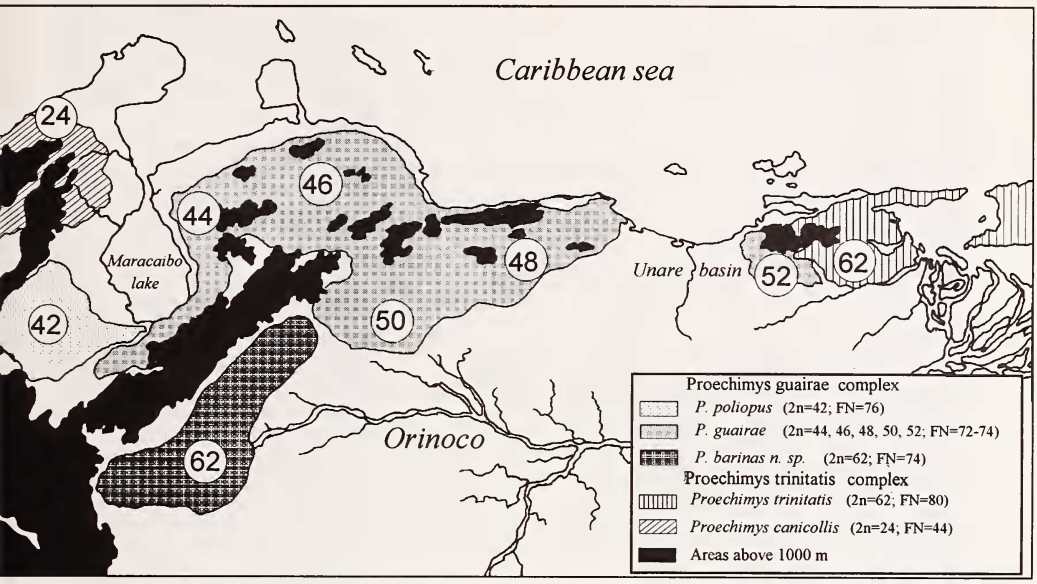

Fig. 1. Map of North Latin America, with the ranges of species and the approximate location of chromosomal races. For the exact location of the localities sampled see Tab. 1

with the highest chromosomal number (2n = 52) occurs in a limited range out of the rassenkreis in the east of Venezuela near *P. trinitatis*. The range is disjunct and separated by the Unare basin (Fig. 1).

There have been some studies on skull morphometrics of spiny rats that focused on some non-geographic aspects of variation, mainly related to growth (Patton and Rogers 1983; Pessoa and Dos Reis 1991a), or on some aspects of intraspecific geographic variation (Dos Reis et al. 1990; Pessoa and Dos Reis 1990, 1991b; Pessoa et al. 1990). However, they refer to other species groups of Patton (1987) such as *P. brevicauda, P. iheringi, P. albispinus, P. dimidiatus, P. guyannensis,* and no analyses are available on the morphometric differentiation of populations and species, namely *casiraguas,* from Venezuela.

The present report describes patterns of morphometric relationships among species and modes of geographic variation in morphometric traits within *casiraguas,* in an attempt to relate these patterns to phylogeny or ecology. Furthermore, we attempt to answer two basic questions: are the karyomorphs morphometrically recognisable with sufficient confidence? Is there any pattern of morphological differentiation that may be interpreted in the light of the established model of chromosomal speciation?

Material and methods

Two-hundred and fifty-five specimens were analyzed representing five species and 12 populations of the genus *Proechimys* in Venezuela (Tab. 1). The species distribution is shown in figure 1 and the exact location of the populations analysed is presented in table 1.

Since the complex displays wide karyotypic variation, most of the animals used in this study were previously karyotyped and correctly assigned to a chromosomal group (Reig et al. 1980; Aguilera et al. 1994) (Tab. 1). Therefore all populations are characterized by their karyotype. Those species and races for which formal description has not yet been carried out will be indicated by us through their diploid number and locality of origin and/or region. These are: *Proechimys* sp. (2n = 62), *P. guairae* "Falcon" (2n = 46), *P. guairae* "Llanos" (2n = 50), and *P. guairae* "Oriente" (2n = 52). *P. poliopus,*

Table 1. **Species and subspecies, locality, diploid number, geographic location (latitude and longitude, acronym and male and female samples)**
Some of the samples were collected from contiguous localities and pooled

Species	Locality	2n	Acronym	Geographic location (latitude and longitude)	Males	Females	Total
P. canicollis	Rio Cachirì	24	*P. can.*	10° 50′ N–72° 13′ W	3	14	17
P. poliopus	Kasmera	42	*P. poli.*	09° 53′ N–72° 43′ W	19	20	39
	Los Angeles del Tucuco			09° 48′ N–72° 50′ W			
P. guairae "Falcon"	La Trilla	46	*P. g.* F	10° 24′ N–67° 45′ W	12	9	21
P. g. guairae	El Limon	48	*P. g. g.* 1	10° 19′ N–67° 38′ W	20	3	23
P. g. guairae	Turiamo	48	*P. g. g.* 2	10° 27′ N–67° 50′ W	12	12	24
P. guairae "Llanos"	Palmero	50	*P. g.* L. 1	09° 44′ N–68° 34′ W	6	6	12
P. guairae "Llanos"	Turén	50	*P. g.* L. 2	09° 16′ N–69° 04′ W	7	7	14
P. guairae "Oriente"	Cueva de Agua	52	*P. g.* O.	10° 10′ N–64° 35′ W	8	10	18
	San Juan de Areo			09° 52′ N–63° 53′ W			
Proechimys sp. (2n = 62)	Guaquitas	62	*P. b.* 1	07° 27′ N–71° 20′ W	12	9	21
Proechimys sp. (2n = 62)	Tierra Buena	62	*P. b.* 2	09° 15′ N–69° 39′ W	14	11	25
	Las Matas			09° 11′ N–69° 35′ W			
Proechimys sp. (2n = 62)	La Nulita	62	*P. b.* 3	07° 19′ N–71° 55′ W	7	9	16
P. trinitatis	Cueva del Guacharo	62	*P. trin.*	10° 10′ N–63° 33′ W	13	12	25

P. guairae "Oriente" and *Proechimys* sp. (2n = 62) Tierra Buena – Las Matas are each represented by two populations (Tab. 1) and have been pooled to increase sample size.

Nineteen distance characters were recorded on the skull and four distance characters on the mandible with the aid of a digimatic caliper (Mitutoyo, 0.01 mm precision). The distance characters are as follows (Fig. 2): Total length (TL): from anterior point of nasal to the sagittal bulge of the occipital; Nasal length (NL): from the anterior point of the nasal to suture with frontal; Basilar length (BL): from the posterior point of the incisor at its alveolus to the anterior border of foramen magnum; Palatal length (PL): from the posterior point of the incisive foramen to the posterior border of the palate; Palatine length (PLL): from the posterior point of incisor at its alveolus to the posterior border of the palate; Upper diastema length (UDL): from the posterior point of the incisor at its alveolus to the anterior point of alveolus M^1; Incisive foramen length (IFL); Alveolar length (UAL): of the upper molar series; Incisor-zygomatic length (IZL): form the posterior point of the alveolus of the incisor to the posterior border of the zygomatic arch; Bulla tympanica length (BTL): longest length of the bulla taken along the axis oblique to the skull length; Fronto-maxillar suture width (FMW); Bizygomatic width (BZW): taken in the widest section; Minimum interorbital width (MLOW): taken over the frontal; Palatal width (PAW): taken in the middle part of the two M^2; Incisive foramen width (IFW): maximum width; Bulla tympanica width (BTW): longest width of the bulla taken along the axis oblique to the skull length; Cranial width (CW): the maximum width taken immediately on top of the external auditory meatus; Maximum height of rostrum (MXHR); Cranial height (CH).

Characters TL, NL, BL, PL, PLL, UDL, IFL, UAL, IZL, BTL, FMW, BZW, MLOW, CW, MXHR, CH correspond to those similarly recorded by Patton and Rogers (1983).

The following four distance characters were recorded on the

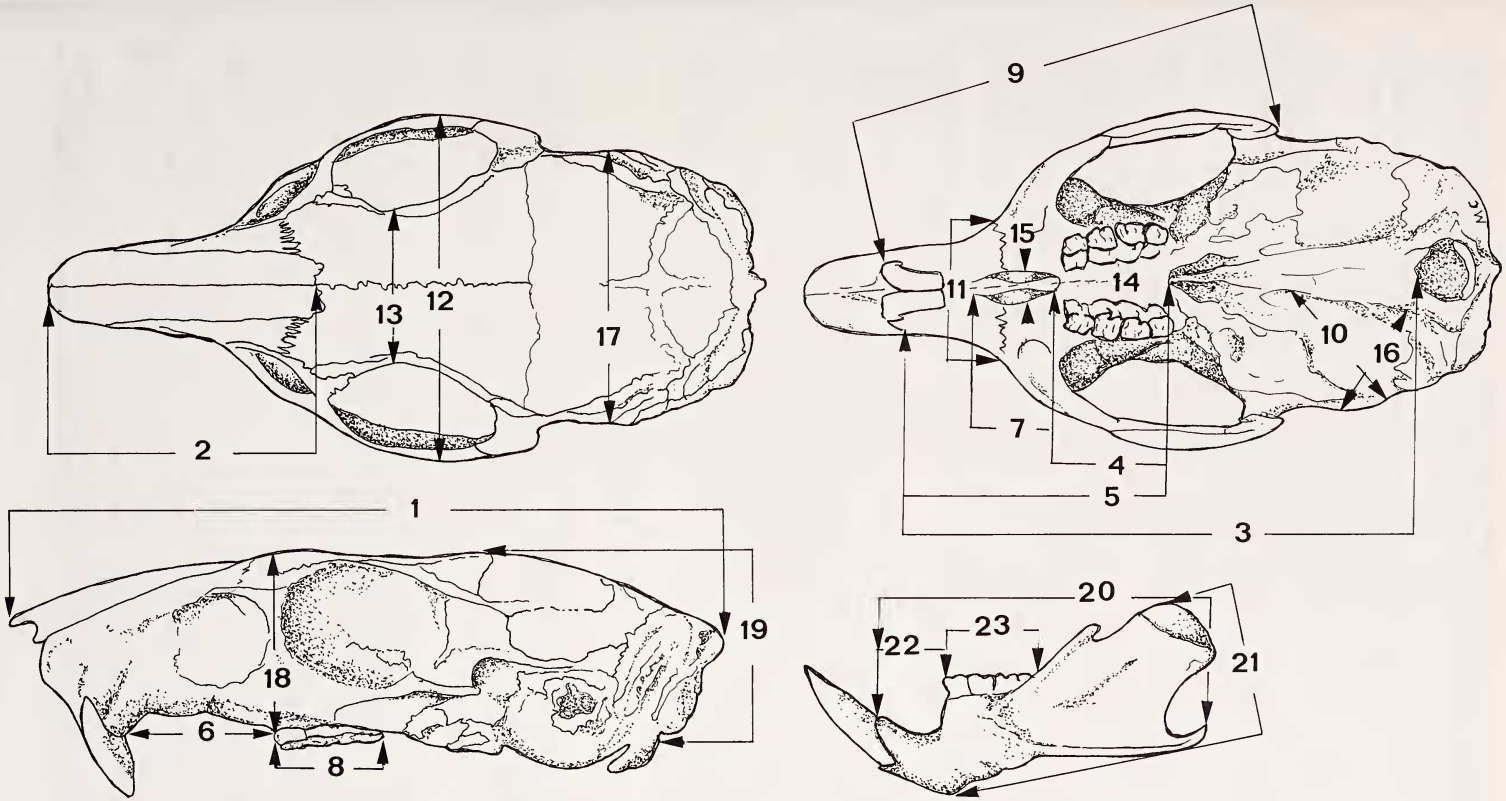

Fig. 2. Characters measured on the skull and the mandible. 1 – Total length (TL); 2 – Nasal length (NL); 3 – Basilar length (BL); 4 – Palatal length (PL); 5 – Palatine length (PLL); 6 – Upper diastema length (UDL); 7 – Incisive foramen length (IFL); 8 – Upper alveolar length (UAL); 9 – Incisor-zygomatic length (IZL); 10 – Bulla tympanica length (BTL); 11 – Fronto-maxillar suture width (FMW); 12 – Bizygomatic width (BZW); 13 – Minimum inter-orbital width (MLOW); 14 – Palatal width (PAW); 15 – Incisive foramen width (IFW); 16 – Bulla tympanica width (BTW); 17 – Cranial width (CW); 18 – Maximum height of rostrum (MXHR); 19 – Cranial height (CH); 20 – Mandibular length (ML); 21 – Mandibular height (MH); 22 – Inferior diastema length (IDL); 23 – Inferior alveolar length of the lower molars (IAL)

mandible: Mandibular length (ML): from the posterior point of the incisor at its alveolus to the posterior border of the mandible; Mandibular height (MH); Inferior diastema length (IDL): from the posterior point of the incisor at its alveolus to the posterior border of the alveolus of M_1; Inferior alveolar length of the lower molars (IAL).

The two character sets were analysed separately. Although in rodents the skull and the mandible form two structures that are highly integrated in their function and during growth, they were analysed independently as they represent sets of genes reflecting different levels of co-adaptation.

Data were transformed into logarithms to render character relationships linear.

The sample includes individuals from both sexes (Tab. 1) and we tested for possible significant effects of sexual dimorphism over the characters by means of two way analysis of variance (unbalanced design), testing for population and sex differences, and for their interaction. A significant interaction of sex with population would suggest that a particular character is sexually dimorphic; therefore, it should be necessary to perform analyses independently for each sex, while no significance would allow the data to be pooled irrespective of sex.

The sample comprises adult animals only, all satisfying 3 conditions: a) M^3 erupted (roughly corresponding to age classes 7 up of Patton and Rogers 1983); b) over 200 g; and c) body length over 200 mm. In doubtful cases, the choice was based upon a combination of a and b or a and c.

Since we recorded a certain variation in size within each population representing static allometry (Klinkenberg and Zimmermann 1992) it seemed essential to correct the data for a proper description of the between group variation. The generally known 'Burnaby' procedure (Burnaby 1966) adjusts original data according to the size vector from the pooled within-group covariance matrix (algorithm suggested by Rohlf and Bookstein 1987). The pooled within-group covariance matrix was then computed and eigenvectors extracted and examined. The first eigenvector was assumed to represent within-group size and the data were adjusted following Burnaby (1966).

Multivariate analysis of variance and canonical variate analysis (CVA) were used to test the 'Burnaby' adjusted data for differences between centroids and to depict a pattern of population variation.

Mahalanobis distances were used to compute UPGMA and to test for congruencies in patterns between the different character sets.

Differences between groups were also investigated for each character through analysis of variance and GT-2 test among means (Sokal and Rohlf 1981). For such practical purposes as the rapid and precise identification of specimens in collections we used the ratios of each character to the total length of the skull in order to identify appropriate measurements.

Univariate and multivariate analyses were performed with the SAS system for the PC (ver. 6.08) using the procedures ANOVA, GLM, CANDISC, DISCRIM as variously modified in Marcus and Corti (1989). A SAS IML procedure from Afework Bekele et al. (1993) was used to adjust original data following Burnaby (1966).

Results

Two-way analysis of variance showed a significant effect of sexual dimorphism in only one out of the 19 skull characters, i.e. IFL (two further characters had $p = 0.055$) and in one out of 4 mandible characters (IDL, Tab. 2). These differences were accepted as negligible and all further analyses were performed by pooling all individuals irrespective of sex. On the contrary, all characters except PL revealed significant differences among populations (Tab. 2).

The eigenvectors were extracted from the pooled within-group covariance matrix of the 19 characters of the skull and examined. The coefficients associated with the first normalised eigenvectors all have the same sign (Tab. 3), and so this vector was taken as representing allometry. Raw data were adjusted following Burnaby (1966) and the new data matrix excluding the allometric effect was subjected to canonical variate analysis (CVA).

The first three canonical variates computed on the skull adjusted data express 59.85 % of total variance (24.35 %, 19.1 % and 16.4 %, respectively). To obtain 90 % of variance it is necessary to reach the seventh canonical variate. However, the variance expressed by the 4th to 7th canonical variates decreases from 11.47 % to 3.96 %, and we accepted the scenario depicted by the first three as representative of population variation.

The population ordination onto these first three variates is shown in the stereogram in figure 3. *P. trinitatis* has the highest score on CV1 and the lowest on CV2, *P. canicollis* has

Table 2. **Skull and mandible characters**

Analysis of variance testing for population and sex differences and for the interaction of sex with populations

Character	Obs.	F	p	Character	Obs.	F	p
TL	234	2.77	.0022	UDL	254	4.79	.0001
		17.62	.0001			13.2	.0003
		1.25	.2555			1.32	.214
NL	236	2.66	.0033	IFL	254	4.39	.0001
		15.65	.0001			4.88	.0281
		1.12	.3434			1.9	.0401
CH	250	7.9	.0001	UAL	256	5.49	.0001
		8.42	.0041			.02	.8805
		1.54	.1187			1.8	.0556
BZW	253	3.59	.0001	FMW	254	7.4	.0001
		10.21	.0016			.49	.4843
		.89	.5546			1.03	.4246
MLOW	256	5.85	.0001	PAW	256	2.08	.0228
		18.44	.0001			.34	.5598
		.75	.69			.54	.872
CW	255	3.51	.0001	IFW	253	3.12	.0006
		12.10	.0006			.58	.4475
		.42	.9477			.58	.8445
PL	256	.83	.6062	BTL	255	6.76	.0001
		.07	.7985			3.33	.0692
		.49	.9093			.96	.4869
BL	248	2.03	.0266	ML	256	3.07	.0001
		12.94	.0004			10.00	.0012
		1.11	.356			1.11	.357
IZL	253	2.57	.0044	IDL	256	19.37	.0001
		8.33	.0043			11.25	.0009
		1.65	.0875			2.45	.0007
PLL	254	4.51	.0001	IAL	256	3.31	.0005
		11.36	.0009			0.03	.0622
		1.51	.1273			1.45	.1500
MXHR	254	5.75	.0001	MH	256	2.95	.0017
		7.99	.0051			3.70	.0532
		1.36	.1949			1.07	.0300
BTW	255	7.49	.0001				
		7.85	.0055				
		1.8	.0554				

First row: population; second row: sex; third row: sex-population interaction, with number of observations, F- value and probability. For character abbreviations see text

low score on CV2. CV3contributes in separate *P. poliopus* with the lowest value and the three *Proechimys* sp. (2n = 62) which have the highest. The *P. guairae* populations have intermediate scores on the three canonical variates. The latter are very similar except for *P. guairae* "Oriente", which has a low value onto CV2.

All between group comparisons are highly significant ($p < 0.001$), as is shown by Hotelling's T^2 on Mahalanobis distances (Tab. 4).

The a posteriori probability of correct classification based upon Mahalanobis distances from group centroids lies between 96 % and 72.73 % (average 87.11 %); most of the incorrectly classified individuals fall within other populations of their own species, thus

Table 3. **19 eigenvalues extracted from the pooled within-group covariance matrix of the skull characters, and the character coefficients associated with the first eigenvector**

Eigenvalues 1–19	Character	Eigenvalue 1 coefficients
36.545	TL	0.489
1.1404	NL	0.239
0.6272	BZW	0.167
0.5703	MLOW	0.059
0.4911	CW	0.096
0.3790	BL	0.399
0.3325	IZL	0.335
0.3214	PL	0.060
0.2980	PLL	0.190
0.2499	UDL	0.129
0.2204	IFL	0.081
0.1913	UAL	0.047
0.1897	FMW	0.091
0.1561	PAW	0.051
0.1161	IFW	0.033
0.1018	BTL	0.076
0.0919	BTW	0.035
0.0807	MXHR	0.104
0.0402	CH	0.034

For abbreviation see text.

suggesting that these distances are a good index of between-species differences. These high values of correct classification decrease when group membership is computed using a Jack-knife restriction (crossvalidate option in SAS) to a range lying between 52.38 % and 88 % (average 69.97 %). However, most of the incorrect classifications are still shared within the *P. guairae* complex.

Although Mahalanobis distances are not characterized by a wide range of variability (2.87–6.04) (Tab. 4), they nevertheless reflect species and population distinctions: *P. trinitatis* and *P. canicollis* have, on average, the highest distances, and the lowest are those between populations of the same species (Tab. 4).

The UPGMA phenogram in figure 4 depicts population relationships based on these distances: *P. trinitatis* and *P. canicollis* are very different, the three *Proechimys* sp. (2n = 62) populations are clustered together and connected with the *P. guairae* complex, which forms a homogeneous group. As also shown by the plot in figure 3, *P. guairae* "Oriente" is remarkably distinct form the other *P. guairae* populations, and in the UPGMA it is linked with *P. canicollis*.

CVA was also performed on the log transformed raw data of the mandible. The first two canonical variates account for 94.55 % of total variation (82.47 % and 12.07 %

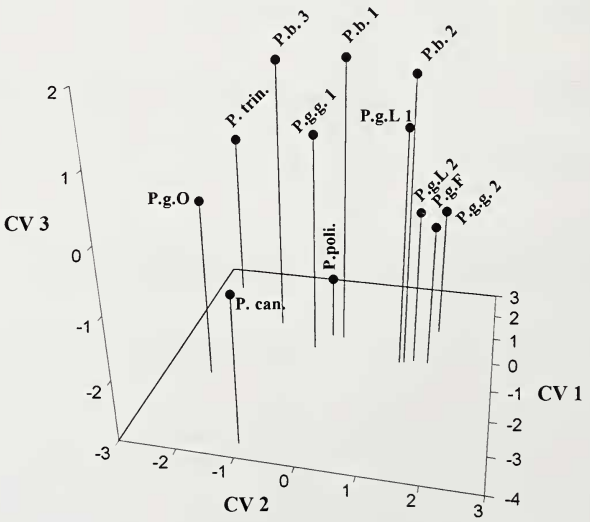

Fig. 3. Stereo scatter plot of population means for the skull onto the first three canonical variates. Units along axes are pooled within-group standard deviations. See Tab. 1 for population acronyms

Table 4. **The matrix of Mahalanobis distances between group centroids for the skull (upper row) and the mandible (lower row)**

Proechimys sp. (2n = 62) (P.b. 1)	—										
	—										
Proechimys sp. (2n = 62) (P.b. 2)	2.87***										
	1.53***										
P. canicollis (P. can)	5.34***	5.20***									
	3.62***	3.69***									
P. guairae "Falcon" (*P.g.* F)	3.56***	3.58***	4.59***								
	1.24**	0.58	3.32***								
Proechimys sp. (2n = 62) (*P.b.* 3)	2.98***	4.07***	5.62***	4.58**							
	1.54***	2.51***	2.44***	2.00**							
P. guairae "Llanos" (*P.g.* L 1)	4.01***	3.78***	5.56***	3.38**	4.35***						
	0.66	1.06	3.31***	0.61	1.56**						
P. guairae "Llanos" (*P.g.* L 2)	4.24***	3.98***	5.51***	2.69**	5.05***	3.25***					
	1.61***	1.71***	2.55***	1.20*	1.41**	1.17*					
P. g. guairae (*P.g.g.* 2)	3.84***	3.75***	5.75***	2.72**	4.80***	4.07***	3.51***				
	1.43***	0.82	3.48***	0.45	2.16***	0.84*	1.14*				
P. g. guairae (*P.g.g.* 1)	3.42***	4.49***	5.15***	3.83**	4.00***	3.49***	3.83***	4.46***			
	0.96*	1.12**	3.15***	0.94*	1.68***	0.76	1.58***	1.37***			
P. guairae "Oriente" (*P.g.* O)	4.08***	4.80***	4.04***	4.91***	4.03***	4.80***	4.88***	5.38***	4.11***		
	4.38***	5.06***	2.03***	4.57***	2.86***	4.31***	3.63*	4.70***	4.27***		
P. poliopus (P. poli)	3.99***	4.37***	5.11***	3.67***	4.16***	4.49***	3.76***	3.56***	4.05***	3.95***	
	1.25***	1.21***	2.64***	0.74	1.40***	0.72	0.91	1.04**	0.77	3.86***	
P. trinitatis	4.52***	5.38***	6.04***	4.92***	4.21***	5.54***	5.59***	5.02***	4.64***	4.69***	4.51***
	0.57	1.01*	3.40***	0.68	1.65***	0.23	1.34**	0.97*	0.62	4.41***	0.81*
	P.b. 1	*P.b.* 2	*P. can.*	*P.g.* F	*P.b.* 3	*P.g.* L 1	*P.g.* L 2	*P.g.g.* 2	*P.g.g.* 1	*P.g.* O	*P. poli*

$p < 0.05$ = *, $p < 0.001$ = **, $p < 0.0001$ = ***, Hotelling T^2.

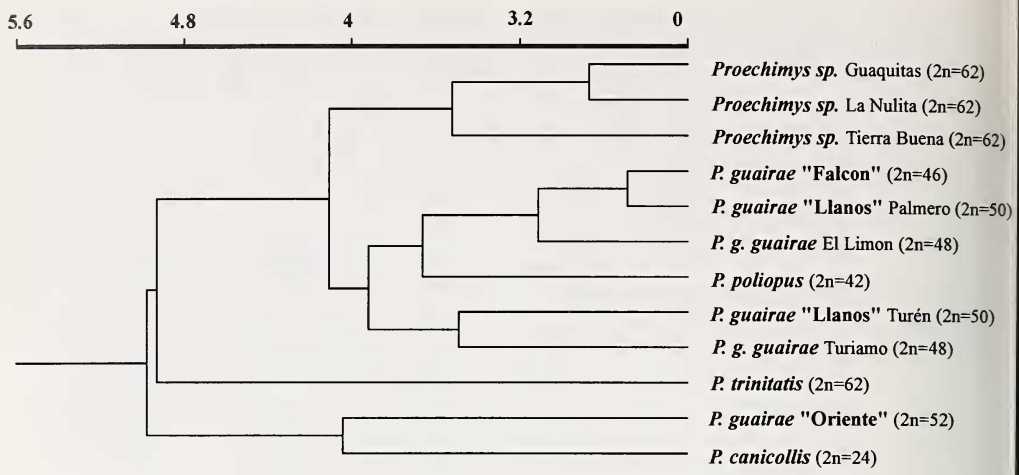

Fig. 4. UPGMA phenogram computed from the Mahalanobis distances between population means for the skull

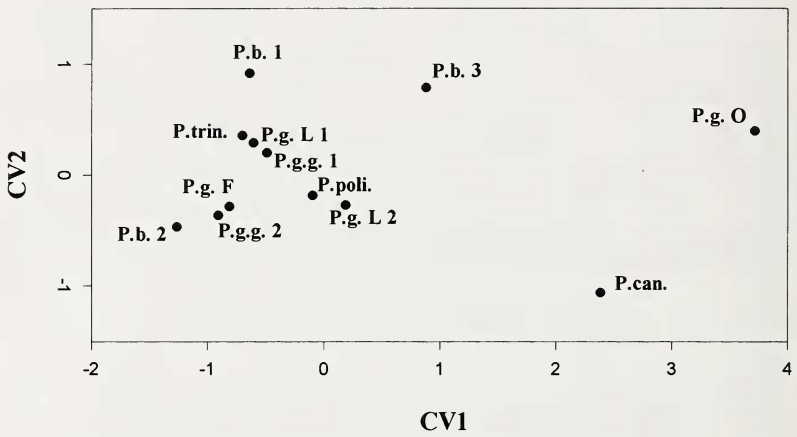

Fig. 5. Scatter plot of population centroids onto first two canonical variates computed on mandible characters. See Tab. 1 for population acronyms

respectively). The scatter plot of population centroids onto first two canonical variates is given in figure 5. CV1 produces a separation of *P. canicollis* and of *P. guairae* "Oriente", which have positive values, from all the others, which have negative values. Lengths of diastema and of alveolar tooth row and mandible height contribute mainly to CV1 and CV2, with pooled within-class standardised character coefficients that are at least 3 times greater than the coefficients of mandible length.

P. guairae "Oriente" and *P. canicollis* have the highest Mahalanobis distances and all are highly significant (Hotelling's T^2, Tab. 4). Distances between the other populations vary without regard to systematic relationships (Tab. 4); for example, Mahalanobis distances between populations of the same subspecies are usually high while distances between populations of different subspecies or species may not be (Tab. 4).

However, a Mantel test between Mahalanobis distances derived from the skull and

those derived from the mandible shows that the two are significantly correlated ($r = 0.388$, $p = 0.0254$), i.e. the analyses on the two skeletal components depict a congruent pattern of population differentiation.

We also performed a Mantel test between the skull Mahalanobis distances and the linear geographic distances measured between the collecting sites. The correlation proved to be significant ($r = 0.358$, $p = 0.0164$). However, the correlation coefficient increases when the test is performed within the *guairae* complex only ($r = 0.40096$, $p = 0.0064$), i.e. when the two allospecies *P. trinitatis* and *P. canicollis* are excluded.

Analysis of variance on character ratios showed that they all differ significantly ($p < 0.01$) except BL, PL, IZL and CW. GT-2 comparisons revealed that significant differences among means are differently scattered, some of the characters exhibiting a homogeneous pattern of differences. There are few significant differences among means within the *P. guairae,* and most of the significant differences are related to the other species. Among these, NL and PAW distinguish *P. poliopus,* UAL, BTL and FMW are unique for *P. trinitatis,* and BTW, IFW and IFL for *P. canicollis.* UDL and CH distinguish *P. canicollis* and *P. guairae* "Oriente" and MXHR *P. guairae* "Llanos", *P. guairae* "Oriente" and *P. trinitatis.*

Discussion

There is no completely positive answer to the first question on the morphometric identification of karyomorphs. Morphometric distinction is clear for those species that have already been recognized and reported in the literature (e.g. Patton 1987; Gardner and Emmons 1984; Reig et al. 1980). Differences in morphometric traits are less evident among the speciating taxa of the *guairae* complex. This is in agreement with the allozyme analysis from Benado et al. (1979) who showed that genetic distances within the rassenkreis are low compared to those with *P. trinitatis* (their *P. urichi;* Aguilera et al 1994).

There is a clear morphometric distinction between *P. canicollis* (the only species forming the *canicollis* group) and the *trinitatus* group. Mahalanobis distances and the UPGMA phenogram clearly highlight this differnce. This is in agreement with Patton's (1987) hypothesis that *P. canicollis* forms a well differentiated group.

Of greatest interest is the *trinitatus* group, in which multivariate morphometrics show a high degree of differentiation among populations. *P. trinitatis* has the highest distinction in skull shape within this group. This species is restricted to a small area in eastern Venezuela and Trinidad island, and morphometric differentiation may be a consequence of a longer time of divergence resulting from the different routes of range expansion of the genus.

Within the superspecies *P. guairae, P. poliopus* (already accepted as a different species by Reig et al 1980) shows a high morphometric differentiation, as well as *P. guairae* "Oriente", which occurs in east Venezuela in a limited area. Moreover, it is interesting to note that the UPGMA based upon skull Mahalanobis distances allows a distinction to be made between the three populations of *Proechimys* sp. ($2n = 62$) and the other subspecies of the rassenkreis. It has been proposed by Aguilera et al (1994) that the former should be considered as a new species, and their morphometric distinction suggests that the trend in the change of morphology of the skull is congruent with their chromosomal differentiation. All populations of the *P. guairae* (i.e. *P. g. guairae, P. guairae* "Falcon", *P. guairae* "Llanos") share the same sort of morphological modifications and the relationships among them are partially congruent with modifications in karyotype.

Some of the character ratios (the ratio between each character and total length of the skull) are of help in identifying the allospecies, i.e. *P. trinitatis, P. canicollis,* and *P. guairae* "Oriente". It is not possible to perform a-posteriori identification of specimens from the *guairae* complex using any individual character as ratio or as raw measurement, and

morphometric distinction is clear only in a multivariate context, as, for example, for the species *Proechimys* sp. (2n = 62) which is clearly distinct.

There is one question relative to morphometric differentiation in this speciose group: Are the morphological changes reported here a by-product of chromosomal speciation, or do they represent independent adaptation to local ecological conditions?

The fact that there is a significant correlation (although not particularly high) between morphometrics and geography across all populations, and that this correlation is even stronger within the *guairae* rassenkreis, indicates that morphometric differentiation originated in the course of the successive events of speciation coupled with chromosomal change. Therefore, our results are in favour of a phylogenetic cause for the morphometric divergence among population and species.

Reig et al. (1980) hypothesized that speciation in the rassenkreis occurred following the stasipatric model of White (1968). In this context, morphometric differences are believed to have arisen in a clinal model where primary integration zones progressively evolved to form tension zones across which gene flow is highly limited if not absent. However, the following alternative model of chromosomal speciation adopted by Reig (1980) and subsequently accepted by Aguilera et al. (1994) favours the hypothesis of speciation via centric fission as essentially peripatric (Mayr 1982), following an increase in diploid number. "This process was repeated several times under the influence of cycles of forest retraction and expansion determined by the Pleistocene climatic fluctuations" (Reig et al. 1980, p. 308). If this is true, morphological differentiation in the superspecies *Proechimys guairae* is a direct product of speciation of small peripheral isolates occurring over the last 50,000 years (Benado et al. 1979).

Acknowledgements

This study has been supported by CONICIT, grant S1-1274 (O. A. Reig and M. Aguilera), by Decanado Investigacines-USB (M. Aguilera), by CNR, Progetto bilaterale "Composizione genomica e speciazione cromosomica nei roditori" no. 93.00233.CT04 (M. Corti), and by MURST, Fondi di Ateneo Università di Roma 'La Sapienza', quota 60 % "Meccanismi di speciazione in ambiente tropicale" (M. Corti).

Zusammenfassung

Kraniometrische Differenzierung und chromosomale Artbildung in der Gattung Proechimys (Rodentia: Echimyidae)

Mittels multivariater morphometrischer Methoden wurden die Systematik und die geographische Variation der Gattung *Proechimys* in Venezuela untersucht. Die erfaßten Populationen zeigen ausgeprägte Unterschiede hinsichtlich des jeweils vorkommenden Karyotyps (2n = 24 – 2n = 62). Die auf Schädel- und Mandibelmerkmalen beruhende morphometrische Differenzierung in der Gattung *Proechimys* unterstützt die Hypothese, daß aufeinanderfolgende Artbildungsereignisse mit einem Anstieg der diploiden Chromosomenzahl einhergingen. Während sich die jeweiligen Einzelmerkmale diesbezüglich als unzureichend erwiesen, waren alle Arten und Unterarten mit multivariaten Verfahren klar unterscheidbar.

References

Afework Bekele; Capanna, E.; Corti, M.; Marcus, L. F.; Schlitter, D. A. (1993): Systematics and geographic variation of Ethiopian *Arvicanthis* (Rodentia, Muridae). J. Zool. London **230**, 117–134.

Aguilera, M.; Reig, O. A.; Barros, M. A.; Basáñez, M. G. (1979): Sistematica, citogenetics y datos reproductivos de una poblacion de *Proechimys canicollis* del Noroeste de Venezuela. Acta Cient. Venezolana **30**, 408–417.

Benado, M.; Aguilera, M.; Reig, O. A.; Ayala, F. J. (1979): Biochemical genetics of chromosome forms of Venezuelan spiny rats of the *Proechimys guairae* and *Proechimys trinitatis* superspecies. Genetica **50**, 89–97.

Burnaby, T. P. (1966): Growth-invariant discriminant functions and generalized distances. Biometrics **22**, 96–110.

Dos Reis, S. F.; Pessoa, L. M.; Strauss, R. E. (1990): Application of size-free canonical discriminant analysis to studies of geographic differentiation. Rev. Brasil. Genet. **13**, 509–520.
Gardner, A. L.; Emmons, L. H. (1984): Species groups in *Proechimys* (Rodentia, Echimyidae) as indicated by karyology and bullar morphology. J. Mammalogy **65**, 10–25.
King, M. (1993): Species evolution. Cambridge: University Press.
Klinkenberg, C. P.; Zimmermann, M. (1982): Static, ontogenetic and evolutionary allometry: A multivariate comparison in nine species of water spiders. Amer. Natur. **140**, 601–620.
Marcus, L. F.; Corti, M. (1989): Data analysis in systematics. Int. Ther. Con. **5**, pp 1–61.
Mayr, E. (1982): Processes of speciation in animals. In: Mechanisms of speciation. Ed. by C. Barigozzi. New York: Alan R. Liss. Pp. 1–19.
Patton, J. L. (1987): Species groups of spiny rats, genus *Proechimys* (Rodentia: Echimyidae). Field. Zool. **39**, 305–345.
Patton, J. L.; Rogers, M. A. (1983): Systematic implications of non-geographic variation in the Spiny rat genus *Proechimys* (Echimyidae). Z. Säugetierkunde **48**, 363–370.
Pessoa, L. M.; De Oliveira, J. A.; Dos Reis, S. F. (1990): Quantitative cranial character variation in selected populations of the *guyannensis*-group of *Proechimys* (Rodentia: Echimyidae) from Brazil. Zool. Anz. **225**, 396–400.
Pessoa, L. M.; Dos Reis, S. F. (1990): Geographic variation in *Proechimys dimidatus* (Guenther) (Rodentia: Echimyidae). Zool. Anz. **225**, 383–390.
— — (1991a): The contribution of cranial indeterminate growth to non-geographic variation in adult *Proechimys albispinus* (Is. Geoffroy) (Rodentia: Echimyidae). Z. Säugetierkunde **56**, 219–224.
— — (1991b): Cranial infraspecific differentiation in *Proechimys iheringi* Thomas (Rodentia: Echimyidae). Z. Säugetierkunde **56**, 34–40.
Reig, O. A. (1980): Modelos de especiacion cromosomica en las casiraguas (genro *Proechimys*) de Venezuela. In: Ecologia y genetica de la especiacion animal. Ed. by O. A. Reig. Equinoccio: editorial de la Univ. S. Bolivar. Pp. 149–190.
— (1989): Karyotypic repattering as one triggering factor in cases of explosive speciation. In: Evolutionary biology of transient unstable populations. Ed. by A. Fontevidela. New York: Springer-Verlag. Pp. 246–289.
Reig, O. A.; Aguilera, M.; Barros, M. A.; Useche, M. (1980): Chromosomal speciation in a rassenkreis of Venezuelan spiny rats (genus *Proechimys,* Rodentia, Echimyidae). Genetica **52/53, 291–312.**
Rohlf, F. J.; Bookstein, F. L. (1987): A comment on shearing as a method for 'size correction'; Syst. Zool. **36**, 356–367.
Sokal, R. R.; Rohlf, F. J. (1981): Biometry. 2nd ed. New York: W. H. Freeman and Co.
White, M. J. D. (1968): Models of speciation. Science **159**, 1065–1070.

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